CONFERENCE OF EMPIRE METEOROLOGISTS, 1929.

AGRICULTURAL SECTION.

The Relation of Weather to Plant Diseases.

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By Wyman & Sons, Ltd., Fetter Lane, London, E.C.4.

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COMMONWEALTH MYCOLOGICAL INSTITUTE

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THE RELATION OF WEATHER TO PLANT DISEASES.

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Introduction.

The object of this paper is to outline briefly the relation of weather to plant diseases, and to suggest methods by which the meteorologist can be of assistance to the plant pathologist. Plant diseases caused by parasitic agencies alone will be considered, and the discussion will be limited to diseases due to fungi and allied micro-organisms.

A century or more ago the diseases of crop plants were attributed directly and solely to adverse weather conditions. At a later period scientists, on discovering that certain micro-organisms were responsible for these diseases, concluded that the previously held view of the direct connection between weather and disease was entirely erroneous. Thus, seventy years ago, neither the plant pathologist nor the agricultural meteorologist realised the essential and true connection between weather conditions and the outbreak and spread of disease in cultivated crops. As the science of plant pathology developed, however, it became evident that in certain years some diseases were conspicuous by their severity and others by their mildness or even complete absence, this order being reversed in other years when different weather conditions prevailed. In more recent times, research on the relation between weather conditions and the prevalence of plant diseases has progressed remarkably, as a result of studies made both in the laboratory and in the field. This "phenological" aspect of plant pathology is, nevertheless, still in its infancy; and not until much more extended data become available can the prevalence of epidemics in crops be correlated with certainty with specific weather conditions. What the plant pathologist really needs is a system of weather forecasting sufficiently detailed and accurate to enable him to advise growers that certain diseases are sure to appear, because the coming weather will be favourable to those diseases. Acting on such advice the grower would then be able to take such preventive measures as were possible to ward off attack.

That a definite connection exists between weather conditions and certain plant diseases can readily be seen in almost any season. In a small country such as England, where there are no wide variations in climate at any time, instances can be given of diseases being unusually prevalent in one year and absent in another. Amongst such diseases are those caused by the Powdery Mildews (*Erysiphaceae*), which became epidemic in the dry, hot summer of 1921. In that year, however, two diseases were noticeable for their comparative absence, namely, Potato Blight, due to *Phytophthora infestans*, and Yellow Rust (*Puccinia glumarum*) of Wheat. Such

2916. Wt. P. 1177—2318. 375. 8/29. Wy. & S., Ltd. Gp. 2.

occurrences show that different diseases are affected differently by the same weather conditions. Countries of very extended area, such as the United States of America, present wide climatic variations; consequently the correlation of plant disease incidence with meteorological factors is more readily discernible.

The various factors which comprise "weather" have been studied, most frequently separately, at some length. A few diseases, such as the Potato Blight and the Cereal Rusts, have been examined from the "collective weather" point of view, but it will be preferable to examine in what ways the individual factors influence the disease-complex first, and then to review and discuss those particular cases afterwards.

Temperature.

In attempting to review our present knowledge of any individual factor such as temperature, it is still too early to explain fully the various phenomena observed. It must suffice here to indicate the phenological relations that exist; chemical and physiological explanations may be left for discussion amongst plant pathologists themselves.

It is natural to begin at a time antecedent to the appearance of a disease, that is, before the pathogen has attacked its host plant. It is now well known that, for the occurrence of an epidemic, it is not necessary for the fungus or other pathogen to be present at the outset in overwhelming numbers. It is sufficient if a small amount of the pathogen is present in a resting or latent form; for this, provided conditions are right, will develop and attack its host plant. Consequent upon this the secondary sources of infection (usually spores of some kind) formed by the pathogen when once established on the host plant, become distributed naturally, often by wind, to other plants. In this way the area of infection increases and an epidemic develops.

Temperature plays a very great part in the initial germination of the spores of the pathogen. In some cases it directly affects its survival through the winter or resting period. Often the survival of a fungus is imperilled by the weather conditions of the previous summer and autumn, which may prevent the formation of the very spores by which it normally survives the winter; or such spores may actually be killed.

This occurred, for instance, at Cambridge during 1921, when the hot, dry summer killed all the uredospores of *Puccinia glumarum*, so that during the winter of 1921 and the spring of 1922 no uredospores could be found (Mehta, 162).* The writer personally noted the absence of this fungus, again, in the winter of 1926 and the spring of 1927, and there is little doubt that the summer weather of 1926 was, at least, partly responsible. Provided that the

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* Numbers in parentheses refer to literature citations at end of paper.

uredospores of *Puccinia glumarum* survive until the beginning of winter, they can easily survive further until the spring, since they are not injured by low temperatures. Miss Sampson (224) collected uredospores of *P. glumarum* in Wales after from 3° to 8° C. of frost during the winters of 1922 and 1923, and found them capable of germinating. Marshal Ward (286) found that the spores of *P. dispersa* on Bromes were killed by high temperatures (30° C.), but that they survived freezing. Mehta (162) found *P. triticina* also capable of surviving freezing temperatures, but the uredospores of *P. graminis* were killed by the lowering of the temperature that occurred in the middle of December. Another worker, Waterhouse (287), recorded the fact that the uredospores of *P. graminis* can survive the high temperatures of an Australian summer.

Again, temperature directly affects the germination of fungus spores. The spores of some fungi seem to need freezing before they will germinate. For instance, Salmon (222) found that the spores of *Sphaerotheca Humuli* germinated better after freezing for twelve hours. Temperature also affects the type of spore germination in some cases. For example, in the Potato Blight fungus, *Phytophthora infestans*, high temperatures cause germ-tube germination, but low temperatures cause zoospore liberation, although it must be admitted that temperature is not the only factor that determines the mode of germination of these spores. Melhus (166) obtained optimum zoospore liberation at from 12° to 13° C., but optimum germ-tube formation occurred at 24° C. The zoospores of this fungus remain motile for twenty-two hours at 5° to 6° C., while they remain motile for only nineteen minutes at 24°–25° C., thus diminishing the chances of infection at the higher temperature. Infection with the Potato Blight fungus is thus dependent upon relatively cool weather. Melhus (164) obtained greatly increased infection when plants were chilled for twelve or twenty-four hours to 10°–13° C. than when they were left at 21°–25° C. Gregory (91, p. 419) also found similar effects with *Plasmopara viticola*, the cause of Downy Mildew of the Grape. This disease starts in cool weather, owing to the fact that the resting spores do not germinate at 80°–90° F., while at 70° F. there is 40–50 per cent. and at 50° F. 95 per cent. germination. At 35°–41° F., however, there is hardly any germination. The zoospores also remain active longer at 50° F., as do those of *Phytophthora infestans*.

With Apple Scab (*Venturia inaequalis*), Keitt and Jones in the U.S.A. have studied the seasonal relations carefully (130). Possibility of infection begins as soon as the tips of the sepals emerge from the fruit-buds, and it lasts until from two to four weeks after petal fall. Again, although it may at no time be absolutely at a standstill, infection occurs readily in the autumn, when fruits and leaves may be attacked if cool moist weather occurs. Although the temperature range for infection is very wide (viz., from 6°–26° C.), the optimum is round about 20° C. The ascospores, curiously enough, germinate

at temperatures of from 0·5°–32° C. It seems, also, that temperature has an influence upon the progress of the fungus in the tissues. Thus, at 8° C., the incubation period was prolonged to seventeen days, as compared with eight to twelve days at 20°–25° C. The disease developed sparsely after thirteen days at 26° C. in one trial, but failed to develop under similar conditions in two other trials. Nevertheless, it is a fact that the fungus tolerates summer temperatures in orchards much exceeding 26° C. It may be that the diurnal rise and fall in temperature has the same effect as a constant lower temperature. Keitt and Jones thought that the temperature range of the host plant exceeded that of the fungus. In any case, it seemed certain that the disease ranged within temperature limits approximating to those endured by the parasite.

Citrus Scab, caused by *Cladosporium Citri*, is a disease the climatic relations of which can readily be studied, because the citrus fruit is grown in so many parts of the tropics that great variations in temperature are associated with its cultivation. Fawcett (62) found that citrus foliage became infected only at relatively cool temperatures, viz., 16°–21° C., and that this range corresponded with the optimum for growth of the fungus in pure culture. Peltier (187) and Peltier and Frederich (192, 193) found a similar range for infection, and correlated the seasonal appearance of the disease with climatic conditions. They found that the warm spring of 1918 in Alabama caused very early growth of the trees, which, by the time the temperature reached that favourable for the fungus, had passed the susceptible stage; hence no Scab was reported there that year. The year 1915, however, was abnormally cold until much later in the season, and host growth was thereby retarded. When growth began, the temperature was also favourable for infection, hence Scab was prevalent in that year. In Manila (Philippine Islands) there is no Citrus Scab, because the temperatures there are too high for infection (mean 27° C). On the other hand, at Los Angeles (California), Mobile (Alabama), and Nagasaki (Japan) Scab is prevalent, because at these places the mean temperature lies between 16° and 19° C., a range that is the optimum for both infection and progress of the disease.

Opinions vary as to the set of conditions necessary for the development of Black or Stem Rust of Wheat, *Puccinia graminis*. Apart from the survival of the uredospores, which has already been referred to, Bolley (17) as well as Freeman and Johnson (65) consider that cool weather is necessary for its development, while Cotton (37), Levine (141), Stakman and Lambert (245) and Walster (285) consider warm weather as conducive to the occurrence of this rust. Stakman and Levine (246) give 19°–21° C. as most favourable for vigorous infection. Heald (91, p. 733) agrees with this and considers that the low temperatures of 1904, in some States of the U.S.A., were responsible for the outbreak of the Black Rust in that year, such low temperatures retarding the crop and giving a chance for the development

of increased numbers of uredospores. Peltier (189) states that infection takes place under conditions unfavourable for the development of the disease, the optimum temperature being 20° C. for one strain tried and 25° C. for another. Infection also depends upon the stage at which the host has arrived ; for, at the heading stage, infection takes place at a lower temperature than at other stages. Johnson (112) recorded the germination of Stem Rust uredospores as being best between 9° C. and 25° C., the optimum, as indicated by the vigour of the germ-tube, being from 12° C. to 17° C. Quite recently Lambert (133) has examined the weather relations to Stem Rust of Wheat by the historical method ; and, although he considers that warm weather in the growing season (May to July) is correlated with destructive epidemics, he nevertheless concludes that there is no evidence of any specific meteorological condition, or set of conditions, that always accompanies epidemics in the spring wheat areas of the U.S.A.

As to Yellow Rust of Wheat (*Puccinia glumarum*) Humphrey has stated that low temperatures are conducive to effective infection by this rust fungus (105). But it is peculiar that its uredospores, which are usually favoured by low and killed by high temperatures, should be able to germinate at 30°–35° C. (Butler and Hayman, 28). More recently Mehta (163) has tested the viability of the uredospores of Yellow Rust at high temperatures, and finds that for India, such spores have no chance of surviving the scorching heat of the summer months in the Indo-Gangetic Plain, where the shade temperature in several localities may occasionally reach 47° C. Mehta found that fresh uredospores of *P. glumarum*, collected in March and having then a 50 per cent. germination, suffered a gradual decline in germinating power from 40 per cent. at 30° C. to hardly 2 per cent. at 47° C. after three hours' exposure. After eighteen hours' exposure to 42° C., all viability was lost. Control uredospores, kept for eighteen hours at 28° C., showed over 30 per cent. germination.

The Leaf Spot of Tomato, caused by *Septoria Lycopersici*, is a well-known example of a warm weather disease. Pritchard and Porte (204) were able to correlate high temperatures with its distribution. It is absent on the Pacific coast of North America and present only sparingly in the North Atlantic and Gulf States ; but it is serious further south, in the Mid-Atlantic and Mid-Western States. This is occasioned by the limited range of temperatures favourable to spore production, namely 15°–26° C., with an optimum at 25° C. The fungus itself also grows over a range of 12° to 28° C. and best at 25° C. The kind of host growth that is particularly susceptible to infection, viz., long, succulent shoots, is produced at higher temperatures (25° to 30° C.) than those at which the maximum yield of fruit and a resistant type of shoot growth are produced. The existence of these two temperature ranges, namely 12°–28° C. for the fungus, and 25°–30° C. for the host should theoretically

induce the development of disease where they overlap, that is from 25° to 28° C. Actually this is the optimum range of temperature found by Pritchard and Porte for the maximum production of the disease.

It was mentioned previously that the Potato Blight starts only at relatively cool temperatures. But after the disease has once made a start, warm weather is necessary for the development of an epidemic. On the other hand, really hot weather is inhibitive, and Blight is usually absent from localities where the mean temperature exceeds 25° C. Smith (237, pp. 234–6) considers that temperatures below 21° to 23·5° C. are most favourable for the spread of this disease, and his contention is rather supported by the growth-temperatures of the fungus in pure culture, which Jones (237, pp. 234–6) gives as being optimum at 16°–19° C. Smith considered that a single hot, dry season may destroy the fungus so effectively, that several successive wet, cool years are needed to re-establish it. Spore production is checked at 25° C. and the mycelium is killed, even in the potato tubers, at temperatures of 30°–35° C. In spite of this, however, Johnson (113) stated that the disease progressed very slowly below 25° C. and was most active at from 25°–32° C., coming to a stop only at temperatures above 36° C.

Air temperature affects the progress of disease chiefly by influencing (1) the rate of growth of the fungus in the tissues of the host plant, and (2) the production of spores. With regard to the first of these, the rate of growth may affect the incubation period directly. Peltier (189) states that at low temperatures *Puccinia graminis* lies dormant in the tissues after infection, and the incubation period may extend over seven to nine weeks. Stakman (246) noticed that uredospores of this fungus appeared in five to seven days after infection at 19°–21° C., but that they appeared one day later for every 10° F. ($5\frac{5}{9}$° C.), rise above, and for every 5° F. ($2\frac{7}{9}$° C.) fall below, this optimum. Mehta (162) examined the influence of temperature on the length of the incubation period in various rusts in 1921 and 1922. He consistently obtained longer incubation periods with lower temperatures. For example, in one experiment plants gave pustules on the thirteenth day at 16°–21° C.; but corresponding plants in the open, at a mean temperature of 1° C., did not give pustules till the thirty-sixth day. Mehta considers it probable that the mycelium does not lie wholly dormant but grows "by fits and starts" according to the variation of the external conditions. While such observations indicate that the mycelium of *Puccinia glumarum* and that of *P. triticina* may thus be able to overwinter as an extended "incubation period," yet experiments have also indicated that *P. graminis* cannot do so unless the temperatures are very mild. Mehta also found that the incubation period is extended by higher temperatures. Yellow Rust developed in eighteen days at the higher temperatures of August, but in nine days in June.

Fromme (67) has also noted this relation of temperature to the incubation period with *Puccinia coronifera*, having observed a decrease of five days when the temperatures reached 20°–30° C. Hart (86) found that higher temperatures diminished the incubation period, but he also found that very high temperatures extended it with *Melampsora Lini* on Flax. At 7°–14° C. pustules appeared in fourteen days; at 16°–22° C. in ten days; while at 25°–30° C. fifteen days were required. Melhus (166) has noted that temperature affects the mycelium of *Phytophthora infestans*, infection becoming visible in two to three days at 23°–27° C., but taking longer at lower temperatures. Keitt (129) found that visible infection of the Apple by Scab (*Venturia inaequalis*) took seventeen days at 8° C. but only eight days at 20° C. Melhus (165), while investigating the problem of the origin of epidemics arising from the planting of infected tubers, found that the extension of the Potato Blight fungus from the tubers into the growing shoots was favoured by a relatively high temperature (22° C.) but that it was inhibited by low temperatures from about 4°–6° C. Since it is still to some extent problematical as to how epidemics of Potato Blight really originate, this point is of interest, since it would indicate that if epidemics start from shoots infected with mycelium derived from infected tubers, the incidence of warm weather would facilitate the primary appearance of the fungus, while cold weather would check it.

Another relation of air temperature to disease may be mentioned, and that is the effect on sporulation. Conidia of the parasite seem to be produced, as a rule, at temperatures optimum for the existence of the disease. For example, Tisdale (262) and Beach (8) state that the conidia of *Phytophthora Nicotianae* and of *P. Cactorum* are formed at 20°–35° C. and a little below 20° C., respectively, at which temperatures the diseases they produce are at a maximum. That temperature, more than moisture, affects the production of the conidia of *Pseudoperonospora Humuli* on the Hop is indicated by Salmon and Ware (223), since they state that in spite of the dryness of the atmosphere during the hot weather of 1923, conidia were found on hop foliage. Again, Walker (278) found that the conidia of *Colletotrichum circinans* (Onion Smudge) were produced at temperatures of 20°–28° C. in appreciable quantities, and these temperatures cover the optimum for the disease (23°–28° C.). Fawcett (62) found that the conidia of *Cladosporium Citri* were produced abundantly only at those temperatures near the optimum for the disease (16°–23° C.), namely at 21°–24·5° C.

The relation of temperature to plant disease may next be considered as it affects diseases contracted from the soil. This is much better known, since there are not so many variable factors to consider as with aerial diseases. There is practically no wind factor to consider, and the soil is slower to gain or lose heat than the air. Also, according to the moisture content of the soil, heat

conservation varies, since water is even slower to gain or lose heat than soil itself. Soil temperatures are more stable than atmospheric ones, and can reasonably be expected to remain near a mean for a twenty-four hour period, thus rendering the meteorological data more reliable for use in phenological work.

One of the principal effects of soil temperature is upon the germination of spores, influencing as it does, both the percentage and the rate of germination. In regard to the rate of germination, Gilman (72) found that the spores of *Fusarium conglutinans* (Cabbage Yellows) germinated in three hours at 33° C., in eight hours at 21° C., in twelve hours at 16° C., but not even in seventy-two hours at 8°–12° C. Shapovalov (231), with *Actinomyces scabies* (Common Scab) on the potato, found that the spores germinated in five hours at 30° C., in eight hours at 25° C., in eleven hours at 20° C., and in eighteen hours at 15° C. ; but required two days at 10° C.

A most noticeable cool weather disease is Powdery Scab of the Potato, caused by *Spongospora subterranea*. It was particularly severe in England in 1920, and that year was cold and wet ; but it was almost absent in the hot, dry season of 1921 (37). Heald (91, p. 368) states that in the cooler northern states on the Canadian border favourable conditions are provided for the disease, but that infected tubers planted in the warmer states (Massachusetts and Florida) yield absolutely clean crops. Ramsey (206) states that in Maine (U.S.A.) the exceptionally hot and dry year of 1916 was very unfavourable for Powdery Scab. Experimentally he obtained 83 per cent. of Scab at 14° C., but none at 17·2° and 24·5° C. As far back as 1908, Massee (153) recorded that the parasite passed from the amoeboid state into the active plasmodial state most markedly at 16°–19° C. On the other hand, while cool weather is favourable, really cold weather is inhibitive to the parasite, a temperature of 10° C. checking its active state and one of 0° C. resulting in its encystment.

Wart Disease of the Potato, caused by *Synchytrium endobioticum*, is favoured by cool weather and it was prevalent in England during the cool year of 1920, but relatively dormant in the dry, hot year of 1921 (37). It has been stated that infection does not occur above 22° C. (73), but it has been shown by Esmarch and Weiss that infection may occur at 30° C. Esmarch (55) found the optimum range for infection to be 15°–20° C. ; and since these temperatures existed in the soil from July to September, they explained the maximum incidence of Wart Disease during that period. At these temperatures, too, the fungus itself is most active ; and while infection does occur at both lower and higher temperatures, it is scanty and retarded, corresponding with retarded zoospore emission from the sporangium. Weiss (291) obtained infection of tubers when resting sporangia germinated between 10° and 28° C. and when summer sporangia germinated between 0·6° and 30° C. He also found the maximum production of disease to occur between 15° and 20° C

The fungus that usually causes the Sleepy Disease of the Tomato in Britain (*Verticillium albo-atrum*) is associated with cool weather conditions, and for this reason is not serious in the United States. In England, it is at times serious in tomato houses. It appears in April and continues to the second week in May, but then disappears till September. This is because of the inhibitive higher temperatures of June to August. Bewley (13) found that by keeping the plants at temperatures above 24° C. they were prevented from wilting ; and above 25° C. the fungus could not infect. At 12·5° C. the fungus grows very slowly up the tomato stems, so that by keeping the plants a little below this temperature they escape infection. The minimum, optimum and maximum temperatures for the fungus in pure culture are 4·4°, 23·3° and 30° C., respectively, and those of the disease are 12°, 21·1° to 22·8°, and 25° C. As the plants thrive best at temperatures between 24° and 29·5° C. it is probable that the fungus is unable to cause infection, owing to resistance developed by the plant above 24° C.

Onion Smut, caused by *Urocystis Cepulae*, is epidemic in parts of the northern States of the U.S.A. but is absent in the southern states. Walker and Jones (281) found that climatic differences accounted for this, the north being cool and the south warm. Onion seedlings appear above ground most rapidly at temperatures of 27°–29° C., but infection does not occur after a certain stage in the host's growth has been reached. This stage is when the cotyledon has reached from $2\frac{1}{2}$ to 3 inches in height. Since increased temperature promotes rapid growth the susceptible period will be shorter at a higher temperature than at a low one. But temperature also affects the germination of the chlamydospores of this fungus. Walker and Wellman (283) found that these spores germinated at temperatures between 9° C. and 32° C., with a maximum germination at 15° C. The same workers obtained maximum growth of the fungus between 18° C. and 22° C, but none at 9° C. or at 28° C. It is significant that infection occurs at temperatures of from 10° C. to 29° C., being maximum at 19°–24° C. Walker and Wellman (284) conclude that while infection occurs at low temperatures, it is not increased appreciably by higher temperatures. Attack, however, is more rapid and is correlated with better host and fungus growth. Above 25° C. the fungus is retarded, while the host is stimulated, so that the susceptible period is rapidly passed.

A large amount of work has been done on the important disease of Wheat known as Bunt and caused by *Tilletia caries*. The spores of this fungus germinate in the soil when conditions are suitable ; and provided the wheat seedling has not passed a certain stage, infection results. The spores germinate at temperatures as low as 5° C. and as high as 25° C., the maximum germination being at 16° to 18° C. (Heuser, 99). Woolman and Humphrey (300) in America found a more extended range of temperatures for germination of Bunt spores, namely, Min. 0°–1°, Opt. 18°–20°, and Max. 25°–29·1° C. ;

but these are probably extreme, as the result of some unusual factor operating in the experiments of these particular workers. Hahne (81), in 1925, gave the following temperatures :—Min. 4°, Opt. 18° to 20°, and Max. 36° C. Still later results by Rabien (205), however, confirm Heuser's figures. The minimum, optimum and maximum for spore germination according to Rabien are :— 5°, 16° to 18°, and 20° to 21° C., but the maximum was extended to 25° C. by the addition of an oxidising agent to the germination medium. The special feature regarding infection is that wheat will germinate at lower temperatures than Bunt spores will. Where this is climatically possible, the solution to the problem of escaping infection is to sow at times when temperatures are very low. Heuser found that wheat grain germinated at 3°–4·5° C. but the Bunt spores did not. Munerati (175) also obtained no infection at 2°–4° C. for the same reason. Gibs (71), on the other hand, obtained infection at 4° C. ; but since the majority of workers have not obtained infection below 5° C., this result cannot be taken too seriously. Munerati found that grain that had germinated and grown at 2°–4° C. was immune from infection, but that this temperature had to be maintained for five weeks to enable the wheat to pass through the susceptible stage unharmed. Grain grown for only twenty days at 2°–4° C. became infected when subjected to a temperature of 10°–12° C. for a further seven day period. It is strange that Rabien obtained no infection when he kept seeds continuously at 10° C. It might be supposed that the wheat could not germinate quickly enough at that temperature to pass the susceptible stage, and that is the only explanation. This is supported by his further statement that two lots of grain kept at 10° C. for three to five days and then transferred to 20° to 22° C., developed 0·7 per cent. and 6·3 per cent. of Bunt respectively ; seed kept at 10° C. for eight days and then raised to 20°–22° C. gave 40 per cent. of Bunt. Also, grain kept at 5° C. for nine days, developed only a trace of Bunt ; but after a longer period, the percentage rose to 49·1. This seems to show that wheat does not grow quickly enough to reach its resistant state, but that at low temperatures the Bunt spores germinate so slowly that they require a long time to infect. Further figures given by Heuser for the host growth seem to support this ; the minimum, optimum and maximum for host growth are :—3°–4·5°, 25° and 30° C. Laufert found that in South Russia wheat sown in August comes up in three to four days, i.e., too quickly for infection to occur, as the spores do not germinate rapidly enough. In Germany, however, temperatures are moderate (6°–10° C.), so that the spores and grain germinate together and infection is the result. This, of course, is contrary to Rabien's results at 10° C.

So much for the minimum temperature for infection. For optimum infection, Hungerford (106) and Gibs (71) give 9°–12° C. and Gibs states that at 17° C. wheat, although susceptible, grows so quickly that the spores, themselves most active, cannot infect.

Faris (59) states that the rate of wheat growth does not affect infection, since he obtained the greatest infection with plants that emerge first. As to the upper extreme, Woolman and Humphrey (300) state that infection from seed-borne spores does not take place when seed is sown at or above 20° C., but that infection from spores in the soil is still possible. This indicates that these authors considered that spores took too long to germinate, when brought into favourable conditions at the same time as the wheat grains, to cause infection ; but that spores, already in the soil with the right conditions, had germinated and were ready to infect when the wheat was sown. Butler (27) states that in India Bunt occurs in the north-west Provinces because the temperatures at sowing time are usually below 25° C., permitting both spore and grain to germinate. But it is absent in the east and south, where the relevant temperatures are above 25° C. at the time of sowing and do not permit spore germination. Munerati (175) found that wheat sown in seed-beds kept at 22°–25° C. for five weeks did not become infected. Grain sown and grown at 2°–4° C. for twenty days and then allowed to grow for a further seven days at 10°–12° C. became infected ; but if this seven-day period was passed at 22°–25° C., infection did not occur. Hungerford (106) found that infection in controlled experiments resulted at temperatures up to 25°–28° C., but at this limit it was almost negligible. In America, farmers are said to escape Bunt in the Pacific North-West by sowing their wheat either very early (warm, above 22° C.) or very late (cold, below 5° C.) (Jones, 124).

As an example of a hot weather disease the ordinary Scab of Potato, caused by *Actinomyces scabies*, may be taken, which was very prevalent in England during the hot, dry year of 1921 (37). There are indications, however, that warm, rather than hot, years are most favourable, for Jones *et al.* (127) state that the optimum temperature for Scab development is about 22° C., although in some trials it was 25° C. Further, the optimum temperature varied with the type of infection ; for the highest percentage of scabbed tubers it was 23° C. but for the highest percentage of total tuber surface scabbed it was 20·5° C. These workers at Wisconsin also found that at 11° and at 30·5° C. scab was very slight. They had previously shown that the number of infections remains as large, above the optimum temperature, as at that point, but that since tuber growth was inhibited, the average size of the Scab lesions was reduced (126). Sanford (227) originally indicated a wider range for maximum infection, viz., from 14° to 22° C., but later (228) he found that, although no Scab usually occurred in the field below 12° C., yet it was not greatly influenced by temperatures between 12° and 25° C. Jones *et al.* (127) state that Scab is worse with more rapidly-growing tubers and that the effect of temperature on Scab is indirect, i.e., through its effect on the host. Sanford (228), in stating that best tuber development occurred at 18° to 21° C., confirms this, since Scab is certainly most pronounced at about 20° C. Although this host

relation is stressed by Sanford and Jones, it is significant that a report on this disease from Ohio (304) gives temperatures for the growth of the organism which almost coincide with those most conducive to Scab. Growth was very slow below 50° F. (10° C.), was maximum at 65°–75° F. (18°–24° C.) and reduced to nil at 80° F. (26·6° C.). Compared with the Scab temperatures as given by Jones *et al.*, namely, 11° C., 20°–23° C., and 30·5° C. the agreement is fairly close.

The Smuts of Sorghum, caused by *Sphacelotheca Sorghi* and *S. cruenta*, are also warm weather diseases, and Kulkarni (132) has shown that the times of sowing and the districts where Sorghum is grown in India determine the prevalence of these diseases. The monsoon crop, sown in June and July, experiences an average temperature of 21°–27° C., which fulfils the optimum infection condition; while the winter crop, sown in September and October and experiencing a temperature of 32°–38° C., becomes much less infected. The scarcity of these Smuts in the Indo-Gangetic plain is explained on this basis, the temperatures there at sowing time being about 32°–38° C. Sorghum germinates most rapidly at high temperatures, taking one and a half days to do so at 37° C.; at lower temperatures it germinates slowly, taking three to four days at 20°–23° C. The spores of these Smuts germinate most abundantly (90 per cent.) at 20°–23° C., but only 1–2 per cent. germinate at 37° C. Infection succeeds at temperatures between 16° and 30° C. Kulkarni tested these observations by pot experiments. Seeds incubated at 40° C. for three days produced no Smut, but seeds incubated three days at 25° C. gave various amounts of Smut. In experimental plots, distributed between four experiment stations, infections resulted only in those plots in which the temperatures at sowing time were below 36° C. At Jacobabad, with a temperature range of 36°–40° C. at the sowing period, no Smut was obtained (131). Reed and Faris (208) obtained similar results. These Smuts are warm weather diseases, since, although the greatest degree of infection does not occur at the highest temperatures, yet the range of temperature for heavy infection reaches a fairly high level. Again, whether the conditions of infection may be called warm or cool depends upon the locality. In India, Kulkarni calls weather favourable to infection "cool," but compared with a climate such as that of England, a temperature of 30° C. would not be called cool.

Moisture.

That the incidence of plant diseases is correlated with the occurrence of wet and dry years had been recognised for a long time before it was realised that this apparent relation could not easily be separated from temperature relations. For example, Potato Blight was practically absent in this country in the dry year of 1919; but was this due more to the absence of rain than to the extreme heat of the weather experienced? It is impossible to answer.

that question off-hand. The weather relations of this one disease alone are too complicated to permit of its incidence being explained on the basis of a single factor. Where it occurred, *Pseudoperonospora Humuli* on the Hop was serious in the wet seasons of 1922 and 1924, but practically negligible in the dry seasons of 1921 and 1923 *Puccinia glumarum* was absent in Cambridgeshire in 1921 also.* But unless the moisture relations of these and other diseases are studied over a much longer period of years, or over a wider range of climates, in order to obtain data as to whether they also appear in hot wet years and in cool wet years, and thus eliminate temperature effect, it is impossible to correlate moisture with disease incidence. On the other hand, it is now possible to carry out experimentally controlled moisture-relation tests, in which other factors, such as temperature, are kept constant. In this way, it has been possible to correlate definitely certain diseases with dry conditions and others with wet conditions. Of these, those occurring in the soil, i.e., in the underground parts of the plants, are by far the most easily studied. Diseases of the sub-aerial parts, such as the cereal Rusts and the Potato Blight, are as yet but imperfectly understood as regards water relations.

As was shown with temperature, moisture has a relation to the overwintering of the spores of fungi. Since more is known regarding this relation in respect of soil fungi, these will be considered first. Some data are available concerning the overwintering of cereal Smut spores. Woolman and Humphrey (300) found that Bunt spores (*Tilletia caries*) overwinter successfully when still aggregated in the form of "butts." As separated spores, however, they lose their viability in one to two months in damp soil. When kept dry for twelve years they have remained viable. Hungerford (106) also regards two to three months as the limit of viability for Bunt spores in damp soil, but he does not put a limit when they remain aggregated. He tested the length of life of Bunt spores in soils having different moisture content, the spores being sown in wet and dry soil, respectively. One series was maintained wet throughout the whole period of the experiment, while the other was moistened only at the time of sowing the spores. Wheat grains were sown at intervals of a few days each. The viability of the spores was measured by the resulting percentage of Smutted plants. Grain sown along with Bunt spores in wet soil gave 30–35 per cent. smutted plants. Grain sown one month after the addition of Bunt spores gave 2 per cent. smutted plants, where the soil was kept continuously moist during the month that elapsed after the addition of the Bunt spores and the sowing of the wheat. But wheat sown one month after

* At the Cambridge University Farm, *P. glumarum* is very late in appearing this (1929) season. It did not appear until June 4th, and had advanced very little by June 21st. This is attributed by Professor Biffen to the prolonged spell of dry weather which has been experienced since the beginning of this year.

the addition of Bunt spores to soil that received no further water after the first day, developed no Bunt. Lastly, wheat sown along with Bunt spores in dry soil gave 19–23 per cent. smutted plants; but sown one month subsequent to the spores, in soil kept continuously dry, it gave only 3–4½ per cent. smutted plants. This indicates that under normal winter conditions, Bunt spores present in the soil from a previous season would not remain viable till the following spring, but would infect grain sown in the autumn. On the other hand, according to Griffiths (78), the spores of Flag Smut of Wheat (*Urocystis Tritici*) can overwinter in the soil, even when previously watered.

Soil moisture also has a very direct influence on the evacuation of the resting sporangia of the potato Wart Disease fungus, *Synchytrium endobioticum*. Esmarch (55) states that evacuation is impeded by dry conditions, but greatly favoured by wet seasons. There are more empty sporangia in spring and summer than in autumn and winter. He also states that oxygen is necessary for this evacuation. Since excessive moisture would bring the oxygen content of the soil down to a minimum, it would be expected that these conditions would inhibit evacuation of the sporangia, but Esmarch does not bring evidence to support any such conclusion. Miss Glynne's experiments (73) also support Esmarch's results, as infection was not obtained in dry soil, while various degrees of infection were obtained in wet soil. The swarm-spores of this fungus, of course, require water in which to swim in order to reach the place of infection. Should the soil dry out before infection has taken place, the swarm spores die.

As to the connection between moisture and oxygen supply, two good examples can be given. With ordinary Scab of Potato, caused by *Actinomyces scabies*, soil water is necessary only in very small quantities, the disease being a dry soil one. A so-called dry soil usually has just enough moisture to allow spore germination and activity of the pathogen; but wet, or at any rate, excessively wet soil as contrasted with merely moist soil, is very inhibitive to this pathogen. Sanford (228) has shown that this is because oxygen is necessary for germination of the spores. The same relation has been found with the Loose Smut of Oats, *Ustilago Avenae*. Miss Jones (120) found that as the soil moisture increased, especially from 60 per cent. to 80 per cent. of the water-holding capacity of the soil, the percentage germination of the spores of this Smut proportionately decreased. In the complete absence of oxygen, germination did not occur, thus confirming the moisture-oxygen relation (121).

With the Powdery Scab of Potato (*Spongospora subterranea*), all agree that the disease is severe in wet seasons only. Ayoutantis (5) states that, in Algeria, this disease occurred as an epidemic in 1922, when an unusually heavy rainfall gave the necessary conditions for its development. Normally, the conditions in Algeria are too dry for this Scab to appear. Ramsey (206) checked his field observations

by controlled glass-house experiments, growing potatoes in pots kept dry, moist and wet, respectively. He obtained no Scab in the dry pots, but 83 per cent. of Scab in the two other series. Even if the low moisture content of the dry soil is sufficient for spore germination, it is evidently not sufficient for infection. That Powdery Scab occurs in soils kept very wet is explainable only on the supposition that oxygen has no influence on spore germination or infection. Infection of potatoes with Wart Disease occurs only with a high soil-water content. But whereas germination of the resting-sporangia does not take place unless the soil is saturated at some time, infection is repressed if the soil is kept constantly saturated (Weiss, 291). Weiss considers periodic flooding and drying most suitable for infection. That a saturated soil is best, at some period at least, is explained by the fact that the swarm spores need water to migrate through the soil to the new crop of tubers.

With *Ophiobolus graminis*, causing Take-All of Wheat, a similar relation of high soil moisture to infection holds good. Here, however, the interacting factors are better known. This disease has been reported by some as serious in dry seasons, by others in wet seasons ; but, as McKinney and Davis (161) pointed out, these reports dealt with the after effects of certain types of weather upon the host plant, and not upon the actual infection process. Wet weather, by causing the plant to develop new roots, defeats the ravages of the fungus from a practical point of view; but the inability of the plant to produce roots in dry weather merely allows the fungus an equal chance of root destruction. The dry weather, which proved fatal to the plants, followed a period of wet weather that had favoured infection. In their experimental work McKinney and Davis obtained less infection at low moisture content than at high ; but whereas the difference was large at high temperatures, it was small at low ones. This indicates that a certain quantity of moisture, which may be considerably below that required for infection, is necessary for the expulsion of the spores of this fungus from its perithecia, or for the germination of spores when liberated.

The disease most widely known as a dry soil disease is the ordinary Scab of the Potato, (*Actinomyces scabies*). Martin, in America, (152) gives data covering three years in which the rainfall varied considerably, and during which varying amounts of Scab resulted. While the temperature was approximately the same for the three years 1920 to 1922, rainfall was lowest in 1921, and for the period June and July was almost half that in the same periods in 1920 and 1922. Correlated with this was almost 100 per cent. of Scab in 1921 and 76 per cent. of Scab in the wettest season of 1920. In control experiments Martin reduced the surface scabbing from 41 per cent., at 30 per cent. soil moisture content, to 2·6 per cent. Scab at 60 per cent. Sanford's results (226), while in agreement with those of Martin, showed that moisture was of influence during the early stages of growth only. If, during this period, the tubers

are kept under nearly saturated conditions they do not become infected, even if the soil becomes dry afterwards. Probably there is enough water present in dry soil to allow growth of the organism and infection ; but with high soil moisture content the tuber must be affected in such a way that infection becomes impossible, because much moisture is favourable to the growth of the parasite (Waksman, 277). It has been stated (304) that the most abundant development of Scab was obtained in light " well-drained," alkaline soil, with a " good supply of moisture." Under such apparently contradictory conditions it is difficult to conclude definitely what may be the decisive factor inducing the disease apart perhaps from the *p*H value of the soil. At low soil moisture content, growth of the organism is reduced, infection is at a maximum, and the plant not very susceptible. At medium moisture content, both plant and organism grow normally and infection is reduced ; while at high moisture content infection is inhibited but the plant made most susceptible. This last condition seems to point to the fact that the fungus is inhibited also, since the plant is susceptible, and plant growth is reduced at low moisture content only because of lack of water. It is rather remarkable that both oxygen content and infection are maximum at low moisture content, while the former is at a minimum, and the latter is inhibited at high moisture content. It thus seems that moisture relations are important only in so far as oxygen supply is affected.

It is commonly stated that if Bunt is to be avoided it is better to sow wheat in a dry seed-bed than after rain. In confirmation of this Hungerford and Wade (107) obtained only a small amount of Bunt in fields sown under dry conditions, but in fields sown soon after rain, 30 per cent. of Bunt appeared. A contrary statement is made by McAlpine (158, p. 91) concerning Flag Smut of Wheat, caused by *Urocystis Tritici*. He states that far more infection results if wheat is sown in dry soil than if it is sown subsequent to rain.

These cases may be analysed and thus further light thrown on the problem. There are four different effects when wheat grains and Bunt spores are sown in a dry seed-bed. Firstly, the dryness may prevent both spores and grain from germinating ; secondly, it may allow the spores to germinate and not the grain ; thirdly, it may allow the grain to germinate and not the spores ; lastly, it may allow both to germinate. The last may at once be dismissed since infection would result, and this does not happen in dry soil if no rain occurs. With Flag Smut of Wheat, McAlpine (158, p. 91) considers that the first relation holds, both grain and spores germinating only when rain comes. He obtained 14 per cent. Smut in dry soil. He placed Bunt in the second category, as he considered that the spores germinated in dry soil but not the grain, the latter doing so when rain came, by which time the spores had germinated and had died (158, p. 80). Kulkarni (132) places the Smuts of Sorghum (*Sphacelotheca sorghi* and *S. cruenta*) in the second category

for the same reason. Many other workers, however, place Bunt in the third category, the grain germinating in dry soil and passing through the susceptible stage before rain occurs enabling the spores to germinate. (*See* 107, 106, 97 and 148.) Mackie (148) states that Bunt spores need 14 per cent. soil moisture in order to germinate. That Bunt spores should germinate in dry soil is not in good consonance with the fact that such spores may remain viable in the soil for years. It is much more natural that they should not germinate in dry soil, and that Mackie's statement that 14 per cent. moisture is needed is correct. Provided that the host plant has germinated, and is still in the susceptible stage, and that the spores are able to infect, the question is whether there is any relation between the degree of infection and the amount of water present, above the minimum.

It has been found that there are two types of correlation ; first, infection increases with increase of moisture, and second, infection decreases with increase of moisture. Bunt of Wheat and the Smuts of Sorghum belong to the first type. With the latter Kulkarni (132) found that below 5 per cent. of moisture, infection did not occur, but it started with 7·5 per cent. of moisture, and increased in proportion with the increase of moisture up to 20 per cent. Hungerford and Wade (107) did not obtain any Bunt below 15 per cent. of moisture, but it increased from 7 per cent. at 15 per cent. of moisture to 62 per cent. at 36 per cent. in one series, and from 25 per cent. at 17 per cent. of moisture to 100 per cent. at 38 per cent. in another series of experiments. Hungerford, in a later paper (106) on combined temperature and moisture relations of this fungus, found that at low temperatures Bunt increased with increase of moisture, but that at higher temperatures it decreased with the increase of moisture. Since temperatures are rarely so high as 17° to 25° C. at the time of sowing wheat, however, one may practically say that an increase of moisture increases the percentage of Bunt. Faris (59) also found that increase of moisture increased the attack of Bunt, although he used spores of *Tilletia levis*. It is of interest, though, that Rabien (205) as recently as 1927, recorded some experiments on the adverse influence of high moisture on Bunt incidence. Wheat in dry soil gave 22·3 per cent. of Bunt, that in normally moist soil gave 55·3 per cent., while that in very moist soil gave only 10·7 per cent. Rabien attributes the reduction of Bunt at very high moisture content both to the rapid germination of the wheat grains and to the retardation of spore germination by the consequent reduction of the oxygen supply. Gibs' (71) observations support the contention that Bunt should be placed in the second type referred to above.

In spite of Hungerford's conclusions regarding these relations, he records two experiments, amongst many others, in which the data support Gibs and Rabien. At the most favourable temperatures of 9°–12° C., which, it must be noted, are " low," he obtained

a reduction from a high infection of 90 per cent. at 22 per cent. moisture to a low infection of 19 per cent. at the higher moisture content of 32 per cent. At the still favourable temperatures of 17°–25° C., a reduction from 21 per cent. infection at 18 per cent. moisture to no infection at 32 per cent. moisture took place. With other fungi of the same class, similar results have been recorded by many workers. Reed and Faris (208) and Kulkarni (132) obtained higher infections at lower moistures with *Sphacelotheca Sorghi* and *S. cruenta*. Christensen (31) found the same with *Sorosporium reilianum*, the cause of Head Smut of Sorghum. Bartholomew and Jones (7), and Reed and Faris (209) obtained higher infection at low moisture with Loose Smut of Oats.

There is a further relation between soil moisture and the progress and intensity of a disease. This is not always separable from the infection relation, and has not received so much attention. A few examples may be given. Soil moisture affects the length of the incubation period. This is rarely examined, as it is very difficult to determine when the first signs of disease appear in the case of soil diseases. Clayton (35) found that the incubation period of Tomato Wilt caused by *Fusarium Lycopersici*, varies according to both temperature and moisture. Here it suffices to state that with 14 per cent. of moisture the period was thirty-five days, with 18 per cent. moisture it was twenty-six days, and with 24–32 per cent. moisture only nineteen to twenty days. This is probably because the greater amount of moisture provides more ideal conditions for the growth of the fungus, and it agrees well with the statement that the most vigorous plants are most attacked.

Moisture can influence the optimum production of disease by reacting on the host. In Crown Gall, caused by *Pseudomonas tumaefaciens*, Riker (214, 216) states that the largest galls are produced at 60 per cent. moisture, and their formation is partly correlated with the best plant growth (at 80 per cent. moisture). With *Plasmodiophora Brassicae*, which causes Clubroot of Crucifers, Monteith (172) found the largest malformations associated with the largest and most vigorous plants, both induced by high moisture. He also found that old and non-vigorous plants were not attacked. These two cases can be explained by the reaction of the host cells to the supply of moisture. In spite of stimulation due to the presence of the respective parasites, the cells could not make abnormal growth if the moisture supply was limited, but they could do so when this was normal.

Another instance of the influence of moisture upon the intensity of a disease is afforded by Cabbage Yellows, caused by *Fusarium conglutinans*. Tisdale (260) found that this disease develops most rapidly at lower moistures (19 per cent.), falling off at 26–28 per cent. moisture; he also found that the host plants grew best at 19 per cent. of moisture and less at higher moistures (261). Tims (259) noted that vigorous plants are most subject to

the disease, and states that plants grown under poor conditions, such as low light intensity and low moisture, will remain for weeks with a low percentage of disease, growing slowly and with thickened tissues. Resistant plants which, under normal moisture conditions carry on as if uninfected, are often in fact infected ; but the fungus is unable to prevail in vigorous plants of a resistant strain. If the moisture content is lowered, however, the plants lose their vigour and the fungus progresses up the plant at once and causes wilt. Such plants will recover if a supply of moisture, adequate for vigorous plant growth, again becomes available. The amount of soil moisture probably has some influence on aerial diseases. Howard (103) states that wheat sown in pots under conditions of good soil aeration had much less Black Rust (*Puccinia graminis*) than those in the field with inadequate aeration. It is more likely that an effect of this kind has to do with atmospheric humidity in the midst of the crop ; but this will be discussed in the next section.

Stakman (246) grew wheat under low and high soil moisture conditions and obtained less infection with low soil moisture. Howard states that flax with deep and abundant roots, when grown in an alluvial soil with good moisture supply, was heavily attacked by *Melampsora Lini*, while flax with shallow roots was free from the rust. Evidently, the shallow roots were able to supply enough water for good growth, but not enough to supply the demands of the parasite or to make the tissues susceptible. This investigator found a similar result with sugar cane ; this host was attacked by *Colletotrichum falcatum* on stiff, black soils (excess water), but was very free from the disease in open porous soils. Smith (239), in discussing the Rust of Asparagus (*Puccinia Asparagi*) in California, states that in dry soils, and in dry seasons, asparagus becomes infected by the uredospores of this fungus in the summer, and from the teleutospores in the autumn. In wet seasons, however, it becomes infected from the teleutospores only, in the autumn. He explains this by the adverse effect of the lack of soil moisture on the plant, which causes it to be more susceptible to the fungus. The latter obtains enough moisture in dry seasons to enable it to infect the host plant, but in wet seasons the fungus is not invigorated in proportion, although the host plant is greatly invigorated and succeeds in thwarting the attempts of the fungus to cause infection. The teleutospores appeared on the plants in the autumn because the plants had then matured and lost their vigour.

Another instance is afforded by the Wheat Mildew *Erysiphe graminis*. This is stated by Rivera (218), in Italy, to be particularly severe when the soil dries out, causing the wheat plant to become more susceptible by the resulting lessening of turgescence. The Mildew is particularly prevalent on plants in rich soils, where root development is relatively restricted, and they would naturally suffer from shortage of water or from excessive transpiration. Fromme and Murray (68) state that soil moisture, as influenced by rainfall, governs

the seriousness of the Angular Leaf Spot of Tobacco, caused by *Bacterium angulatum*. With high soil moisture, the resistance of the plant becomes reduced and infection is increased in proportion.

Atmospheric Humidity and Precipitation.

These factors were for a long time neglected, but lately much study has been devoted to them. At the outset it must be realised that the effect of atmospheric humidity is largely bound up with other factors, such as temperature, light, wind, rainfall, crop density, clouds and the physical nature of the soil. The interaction of all these factors on the physiology and metabolism of the plant is too complex for discussion here, and the various explanations that have been given of the incidence of disease as influenced by atmospheric humidity cannot be dealt with in any detail. It must suffice for present purposes to call attention to the existence of relations between humidity and disease, and explanations must await the securing of more data.

Passing over the obvious ways in which atmospheric humidity or its absence may influence the hardness or softness of tissues, their turgescence, and so on, it can be shown that susceptibility to disease may be related to the effect of humidity on stomatal movement. Pool and McKay (200) demonstrated this with the Leaf Spot of Beet, caused by *Cercospora beticola*, in which infection can take place only through the stomata. High humidity favours their opening, but low humidity favours closure, the degree thus enabling infection or preventing it.

There is also some evidence that humidity affects the survival of fungus spores, such as certain conidia and some Rust spores. Hart (86) for example, found that the uredospores of *Melampsora Lini* (Flax Rust) remain viable longer at relative humidities of about 60 per cent. than at lower ones, and their viability is reduced at very high and very low humidities. Spaulding and Gravatt (243) found that the sporidia of *Cronartium ribicola* require a moist atmosphere in order to remain viable long enough to cause infection, apart from their need of dew or rain for germination and infection. They survived for twenty-six hours at 70 per cent. humidity, but rapidly lost their viability in drier air.

The literature concerning the germination of fungus spores is far too voluminous to review here. All of the many kinds of spores need different degrees of humidity and water-films. The conidia of the Peronosporales, for example, are dependent upon the presence of actual water-films on the foliage, since the swarm spores are capable of causing infection only after a period of swimming in a water-film. Doran (49) reviewed the literature of this problem in 1922. Patel (186) showed that the conidia of *Peronospora Trifoliorum* would not germinate on dry slides in a saturated atmosphere, but did so in a film of water. Melhus (166) showed that the same was true for those of *Phytophthora infestans*.

With regard to Rust spores, most investigators have found that uredospores germinate only in liquid water, and not in saturated air (Doran, 49). Teleutospores such as those of *Cronartium ribicola* also need water (Spaulding and Gravatt, 243); aecidiospores also, such as those of *Melampsora Lini* (Hart, 86); further, sporidia, such as those of *Puccinia graminis* require water (Doran, 49). Although Fromme (67) states that very high humidity was necessary for the germination of the uredospores of *Puccinia coronifera*, he obtained only 6 per cent. infection as a result of 93 per cent. humidity, and this is quite at variance with Durrell's statement (53) that the almost identical rust, *P. coronata*, depends on actual water for germination. Two other exceptional results in regard to germination are those of Smith (238), who obtained 54 per cent. germination with the uredospores of *Puccinia Sorghi* in moist air at 100 per cent. humidity, and those of Taubenhaus (253) who obtained germination of the teleutospores of *Puccinia malvacearum* in moist air also.

There is also a correlation between precipitation and relative atmospheric humidity and the expulsion of spores from the fructifications of many fungi. The pycnospores of *Endothia parasitica* (the Chestnut Blight fungus) are stated by Heald and Gardner (92) and by Studhalter and Heald (252) to be ejected both during and after rain. Smiley (236) showed that fungi, other than members of the Ascomycetes, discharge their pycnospores during rain, e.g., *Phyllosticta Antirrhini*. Although ascospores are also discharged during rain, the condition of the air very soon after the cessation of rain influences the continuance of the expulsion. For example, Heald and Walton (96) found that the ascospores of *Endothia parasitica* are dependent not only on the soaking of the perithecia by rain for expulsion, but also on the relative humidity of the air when the rain stops. Unless the humidity remains very high, expulsion ceases, and it diminishes in proportion to the rate of fall of the relative humidity. The length of a period of dry conditions, too, influences the capability of perithecia to discharge their ascospores, as for example in *Endothia parasitica*. With this fungus, Heald and Studhalter (95) found that the longer the perithecia were exposed to desiccation, the less able they were to liberate their ascospores when favourable conditions of moisture returned. The longer this period of desiccation, the longer was the interval between the onset of favourable conditions and the resulting first expulsion. If this desiccation period were indefinitely prolonged, a point would ultimately be reached at which the return of favourable moisture conditions would no longer cause reaction. This follows because, on the average, the necessary length of period of conditions favourable for expulsion would be less than that required by the delay caused by the extended desiccation period. The above writers state that this absolute inhibitive desiccation period is about three months. The desiccation does not affect the power of the spores to germinate, but merely influences their expulsion.

In the apple Scab fungus, *Venturia inaequalis*, the discharge of the ascospores from the perithecia depends upon rain. Keitt and Jones (130) state that the presence of dew is not enough, but that the ejection of ascospores was always traced to the beginning of rainfall. They further state that it is impossible at present to be sure that the spores cannot germinate without liquid water, since the methods of experimentation under conditions of high humidity do not preclude the possibility of the presence of minute quantities of liquid water. Both Aderhold (2) and Wiltshire (296) stated that the germination of these spores did not take place in a saturated atmosphere.

Whether infection will take place or not also depends on how long moisture remains on foliage. Peltier and Frederich (192) state that the Citrus Scab fungus, *Cladosporium Citri*, needs water on the foliage for a considerable time before infection takes place, infection being a matter of hours and not minutes. Keitt and Jones (130) showed that the wetting of apple foliage, required for infection by *Venturia inaequalis*, must be extended and continuous, and the period varies with the temperature, viz., at 6° C., thirteen to eighteen hours; at 9° C., nine to eleven hours; at 15° C., eight and a half hours; at 20°–24° C., four to six hours, and at 26° C., eight to ten hours. Discontinuous wetting, nevertheless, seems to be an advantage, since the germ-tube in the dry period has an opportunity to adhere to the surface of the leaf by the formation of an appressorium. Hart (86) states that for the infection of flax by *Melampsora Lini* abundant moisture is of no use if it does not remain for more than one and a half hours. On the other hand, a small amount of water is sufficient for slight infection, provided it lasts for three hours; but for the occurrence of severe infection, over twenty-four hours are needed. Tehon and Young (258) observed that *Puccinia graminis* appeared on wheat more or less consistently whenever a certain amount of rain occurred from five to seven days prior to the first symptoms.

The period during which rain occurs also varies in its effects. Moreland (173) found that in India the amount of rainfall at seeding time is not related to attack of cereals by Rusts. Of records at three places, Rusts followed in seasons following wet Octobers in seven instances, but they followed dry Octobers in six other cases. He found, however, that rainfall in January and February was related to Rust infection, since it influenced the state of atmospheric humidity. High rainfall and cloudy weather were conducive to high humidity, and whenever this combination occurred Rust followed. Beauverie (10) states that *Puccinia glumarum* is a Rust of early host growth combined with wetness; *P. graminis* a Rust of wet seasons but appearing late in the season, and *P. triticina* a Rust of dry years, tending to appear towards the latter part of the season. Later, he (11) discussed the occurrence of a violent epidemic of *P. glumarum* in 1923 in Auvergne (France). That year was abnor-

mally wet early in the season (three inches of rain fell in April as against the normal two inches) but later became dry, about the time of ear formation. Early in that year the high rainfall and high temperature caused precocious growth, and this was the condition most suitable for attack by *P. glumarum*. His observations are supported by Foex (64), who, however, is reticent in drawing definite conclusions.

Concerning the humidity factor very definite indications have been obtained by Stoughton (250) with the Angular Leaf-Spot disease of Cotton, caused by *Bacterium malvacearum*. Infection was only slight at the high temperature of 32° C. with over 80 per cent. relative humidity, but with the same humidity at 24°–28° C. moderate to heavy infection resulted. Moreover, with a lower humidity of 70 per cent., even at the same favourable temperatures of 24°–28° C., infection did not occur. Here there is no doubt about the influence of humidity. Roussakov (220) as well as Pool and McKay (199) consider that rain in the open field helps to increase the humidity amongst the crop plants, this being higher than in a dry season when the soil dries out. But the former writer goes further and discusses the time of occurrence of the rain, stating that rain in the daytime does not conserve humidity but lowers it, therefore increasing the effect of rain during the night which does not lower humidity. Both he and Pool and McKay observe that the atmospheric humidity prevailing in the midst of the crop plants is different from that in the open air at about five feet above the crop. It varies not only in this way but also within the crop itself, usually being greater near the soil and decreasing with ascent above soil level (221). Similarly, the density of stand of the crop affects the humidity and thereby the intensity of disease. Butler (27) noted that Yellow and Brown Rusts were severe in the middle of a wheat crop at Pusa, India, where the crop was dense, but there was no Rust on the borders of the same crop where the stand was much less dense. The humidity was 20 per cent. higher in the dense part of the crop than on its borders. This is in agreement with Moreland (173), who recorded bad Rust attacks in three years of over 80 per cent. humidity, some Rust in one year with 79·5 per cent humidity (all four records being at Allahabad, India), but no Rust below 67 per cent. humidity at Jhansi.

It is peculiar that the Mildew *Erysiphe graminis* should be able to cause infection at relatively medium humidities, 75–80 per cent., as found by Fromme (67), but Butler states that the allied fungus, *Erysiphe Polygoni*, causing Pea Mildew, is more prevalent in India in dry years ; it may be that these Powdery Mildews have a considerable power of adaptation to varying conditions. In any case, sufficient data are not yet at hand to correlate any one, or a series of conditions, with incidence of these Mildews. Rivera (218) has put forward a theory concerning the alteration of conditions causing respectively turgescence and wilt. These he considers sufficient to explain the

incidence of Powdery Mildews, but at present not enough data are available to establish his contention.

Butler (27) has pointed out the relation of dew to several diseases, the most important of which is the Potato Blight. In India the disease is endemic only at from four to seven thousand feet above sea level, and it is normally absent from the plains. This is bound up with temperature conditions and the resulting deposition of dew. In 1912 "seed" was brought from these altitudes to the plains rather late, and as the temperature was unusually low, and fogs and dews also occurred in December, the result was a Blight epidemic in January, 1913. His observations are supported by those of Reed (210) in America, who states that, in Virginia, Blight is absent below two thousand feet, but gets more and more severe the higher the crop lies above that height. This is because the more highly situated the crop the cooler the nights (and also the greater the difference between day and night temperatures), and therefore the more copious the deposition of dew. The Die-Back disease of Chillies (*Vermicularia Capsici*) in India, studied by Dastur (39), is also dependent upon dew, and Dastur states that the humidity necessary at the flowering time is above 80 per cent. Whenever the humidity falls below this point in September, the disease does not appear. As the season advances beyond November, the disease disappears, because the lowering of the day temperature prevents the deposition of dew at night. Massee (154, p. 13) suggested that whenever infection was proved to take place only at night, this was because dew is deposited only at night. He tested this by tying healthy Marrow plant leaves in paper bags, six being left exposed and six protected in the bags during the day, while at night the conditions were reversed, those protected during the day being exposed during the night. Only those leaves exposed at night became infected by spores of *Sphaerotheca Humuli*. He suggested that in addition to the presence of a film of moisture on the leaf at night, the cells of the leaf were fully distended with liquid (because of retarded transpiration) and contained more sugars then than during the day, thereby offering ideal conditions for infection.

Light.

Light, being essential to the normal metabolism of all green plants, must indirectly be connected with the occurrence of parasitic diseases. Any factors that tend to alter in any degree the normal light relations of a plant, must tend either to predispose the plant to attack by disease or to confer resistance. Two important ways in which light affects plants are in the photosynthetic process, and in transpiration. Light may also be related directly to the disease producing organism. Most bacteria are killed by intense light and certain fungus spores may be killed by strong sunlight. Hart (86) states that infection of flax by *Melampsora Lini* is independent of light, but Stakman (246) found some reduction of infection of wheat

by *Puccinia graminis* with greater light intensity. Light has probably an important influence on the production of certain fungus fructifications. Hammarland (84) states that light is essential for conidial production in several species of *Erysiphe*. Davis (41) with *Ophiobolus graminis*, the Take-All disease of wheat, says that light favours perithecial formation, while Coons (36) states that light is absolutely essential for pycnidial formation in *Plenodomus fuscomaculans*. Hart (86) found that the pustules of *Melampsora Lini* on flax appeared most rapidly when light was continuous, but that the incubation period was lengthened by alternating light and darkness. In some cases light may increase the temperature of plants. Stevens (249) has shown the temperature of plant tissues to be several degrees higher in sunlight than when shaded. Leaves shade stems to some degree, and Stevens found that the temperature of certain Blackberry canes, shaded by leaves, was 27°–29° C., while that of the unshaded canes was 31°–35° C., the air temperature in the shade in the experiment being 26°–27° C. The stems of some plants, such as potatoes, are much more shaded than those of others, e.g., blackberry canes, and this feature is of importance when using field data.

It is an interesting fact that alternating clear and clouded skies produce a higher temperature on exposed plant tissues than a continuously clear sky, the reflection from the clouds causing the difference. In connection with this shade factor, two or three diseases may be mentioned. With "Yellows" Shapovalov and Beecher (233) found that tomatoes artificially shaded were less infected, that the incubation period was lengthened, and that the plants grew away from the disease even though previously infected, as compared with non-shaded plants. It was supposed that shading lowered the rate of transpiration. Trelease and Trelease (268), working with wheat mildew (*Erysiphe graminis*), found that intense light prevented the disease, while shading the plants allowed heavy infection to occur. This disease is rarely found in the open fields in the United States, and Butler (268) states that in India the Mildew has been seen causing serious damage only in half-shaded plants. Trelease and Trelease ascribed the prevention of Mildew by strong sunlight to a direct inhibition of the fungus or to the greater evaporation and consequent drying of its conidia and mycelium. But they did not record any experiments in which direct sunlight was still allowed to fall on the leaves, under conditions where high humidity, in spite of high temperature, was possible all the time. With Fusarium Wilt of the Potato (*F. oxysporum*), Haskell (89) found that the disease was almost absent where the crop was shaded by an elm tree. Bewley (13) notes that by shading tomato plants the temperature is lowered. But whereas the lower temperature is more favourable for the Wilt fungus (*Verticillium albo-atrum*), generally prevalent in English glasshouses, the host plant does not wilt because of lowered transpiration. It is also

likely that Haskell's disease also entails reducing wilting rather than actual inbitition of the parasite.

There is a more definite relation between light and infection, and that is in connection with the deposition of dew. It is stated that certain diseases are prevented by shading off the heat rays of the sun, thus preventing dew deposition. The diseases in question are Asparagus Rust (239), Celery Blight (*Septoria Apii*), Ginseng Blight (*Alternaria Panax*), and Strawberry Leafspot (*Mycosphaerella Fragariae*) (Duggar, 52).

Wind.

There is no doubt whatever that wind is an agent of dissemination of both fungi and bacteria. After being liberated from their place of origin, spores and bacteria are carried up by air currents into the wind proper. The actual details of what happens to spores afterwards are not known. Only very recently have any data been collected which prove the carriage of spores by wind over any large area or to any great distance. It has been noticed for some time, however, that diseases seem to spread in the direction of prevailing winds. McAlpine, as long ago as 1906, quoted Halsted's observations on the spread of Asparagus Rust (157, p. 7). A field which had been cut to allow the new growth to escape *Puccinia Asparagi* was found to be infected five weeks later. Curiously enough, however, only one side of each plant was affected, and this side consistently faced towards an old and badly infected field of Asparagus. Also the crop standing behind an old house was almost free of infection. The wind had blown in a direction from the old infected field towards the new crop and over the house, and the latter had prevented the spores of the fungus from reaching the crop just behind it.

Woolman and Humphrey (300) showed the relation of wind to the spread of Bunt in a similar way, in the Pacific North-West (U.S.A.). Carsner (29) also gives details of the spread of *Bacterium lacrymans* on cucumber, and Atanasoff (4) of *Gibberella Saubinetii* on rye.

Spores have been caught at various heights by "vaselined" slide traps exposed from aeroplanes. Stakman *et al.* (244) were the first to exploit this method, and they found many kinds of spores even up to a height of 10,500 feet. In England, Dillon Weston (47) has followed this lead. He found, as would be expected, that the nearer the surface of the ground the greater was the number of spores caught. At 9–10,000 feet bacteria only were caught. In summer much greater numbers of fungus spores and bacteria were caught than in the winter months. Some evidence was also obtained that clouds are more heavily charged with spores and bacteria than the air just below them.

The distance to which the spores of fungi can be carried is very important, especially in connection with the epidemiology of plant

diseases. Stakman *et al.* (244) found that the number of spores diminished the further they were caught from the centre of infection. Heald *et al.* (94) proved that the spores of *Endothia parasitica* could be carried in large numbers to a distance of three to four hundred feet from their point of liberation, and considered that they might be carried much further. Snell (240) reports a case in which Ribes bushes became infected by the aecidiospores of *Cronartium ribicola* from a source which was one and a quarter miles away, and in which the carriage of the spores could have occurred only by wind. Butler (26) discussed the relation of wind to spore dispersal and considered that the power of the wind to carry spores for very considerable distances has usually been exaggerated. He states that Bunt spores were not found at a distance of 250 yards from heavily infected fields in Russia and in Germany, although these spores fell copiously at a distance of 440 yards from an infected crop at Pullman, U.S.A. He also quotes the case of *Coleosporium euphrasiae*, the spores of which travelled in the air across water for a distance of five to eighteen miles and caused the infection of plants on islands.

Organised work has recently been carried out in Canada (79, 80) to ascertain the line of distribution of the Black Stem Rust (*Puccinia graminis*). In Manitoba and Saskatchewan this rust was epidemic in certain years, of which 1927 was one. In Alberta the Rust was not so severe in that year. By careful distribution of spore-traps in the areas concerned, however, the amount and the dates of arrival of the Rust spores were discovered. The first infections occurred at Winnipeg and Morden, in Manitoba on July 6th, and subsequently Rust became general, as far north as Winnipeg and throughout south-eastern Saskatchewan, by July 18th. Afterwards it was traced in an epidemic course further north and westwards. In Alberta, epidemic infection did not occur, because of the greater distance the spores had to travel and because the prevailing winds were not east or south-east. Since conditions in Canada are not suitable for the over-wintering of the fungus, and since the possibility of infection from Barberry is stated to be negligible, it is concluded that primary infection arose from uredospores carried by winds coming from a region of infected fields in the United States south of Manitoba and eastern Saskatchewan, situated in the Dakotas and Minnesota. The data obtained with the aid of spore-traps in aeroplanes were instrumental in establishing the fact that rainy weather effectively clears the air of Rust spores, since few were caught in wet weather. In any case, observations which are being continued each year in Canada tend to prove that the wind is responsible for introducing Rust spores from the United States, as was maintained some years ago by Miss Newton (179).

Mehta (163) has made observations, but of a general type only, on the appearance of Yellow Rust in the plains of India. The survival of this Rust occurs every year in the hilly districts, for example, at Muktesar, because of the cooler weather, and is accom-

plished on self-sown plants. Infection of the crop in January easily takes place. The spores of the Rust are believed to be carried by wind to the crops in the plains, a matter of a few miles only (the circuitous hill-paths from Muktesar to the plains are 28 and 24 miles). But the wheat-crop is not up before mid-November and the weather is then too cold in the hills to allow the fungus to sporulate. By January, the weather is warmer, and spores are formed, which are carried to the plains. In no other way can the infection of the crops in the plains be explained.

McCubbin (159) attempted to calculate the distance to which spores of *Cronartium ribicola* could be carried by wind. He found that the most slowly falling spores took from four to five minutes to descend eight feet. By calculation, he determined that a thirty-mile wind would carry spores, starting at a height of eight feet, two and a half miles before they reached soil level, and that they would travel ten miles if liberated from a "hill" thirty-two feet in height. Weston (294) calculated that the spores of *Sclerospora philippinensis*, falling nearly twelve feet in six seconds, would be carried only eighty-eight yards by a thirty-mile wind, before reaching the soil level. In nature it has abundantly been demonstrated that spores may reach a height of ten thousand feet and more. At such heights, spores should be carried hundreds of miles by moderate or strong winds. Whether they are able to infect plants after travelling at such heights and under all conditions of weather, is not known at present, although Stakman (244) states that altitude had no influence on the viability of the spores recovered at great heights. He had, however, no means of knowing for what period the spores had been in the air or of estimating the influence of the duration of this period on the spores themselves.

General Review.

In the foregoing sections, it has been shown for some of the more important diseases of crop plants that each meteorological factor may have a more or less specific influence on the incidence and intensity of such diseases. In regard to some of them, it is true, there are conflicting observations, and to arrive at a definite conclusion as to the phenological relations of the diseases is as yet impossible. For others, however, the data seem to be sufficiently corroborative as to permit the conclusion that phenological correlation is possible.

For some diseases it is possible to state that when atmospheric and soil temperature and moisture conditions fall within certain limits, then disease is certain to occur, assuming, of course, the presence of the parasite. At present, it is not possible to forecast the intensity and duration of epidemics, even though it may be possible to forecast that they will occur.

During the last few years, several countries have organised systems of forecasting the incidence of certain plant diseases, with

the object of warning growers when to begin direct combative measures. France has started the practice of warning growers by informing them when the meteorological conditions indicate a possible outbreak of certain diseases and pests of the vine. At Montpellier, observations are received from fifty-nine outposts in the surrounding region, and also from other parts of France and abroad. By combining these with observations on crops at the station, advice is sent daily to subscribers as to the advisability of preventive treatment. This scheme has been in operation since 1923, and there are indications that the work is successfully fulfilling its objects (Chaptal, 30).

A similar system has been in vogue in Italy since 1921, with the main object of forecasting attacks of Downy Mildew (*Plasmopara viticola*) on vines (Voglino, 275). Observers are scattered over the three provinces of Turin, Cuneo and Novara, and their reports are sent to the Central Phytopathological Station at Turin. Advice is issued immediately meteorological conditions indicate that germination of the winter spores of the fungus and infection of the vines are probable.

In Germany, a centre was established some time ago, where reports of meteorological conditions and of crop diseases could be received. There the data are sorted and examined to find correlations between the diseases and the weather (293). The United States Weather Bureau also carries out phenological and plant pathological observations; and, for a few diseases, such as Potato Blight and Apple Scab, close correlations have been obtained. Recently, both in America and Canada (Güssow 79, 80), reports have been issued relative to the first expulsion of ascospores from the perithecia of the Apple Scab fungus, and advice given as to the advisability of spraying. In Holland, too, attempts have been made fo forecast the incidence of Potato Blight (van Poeteren, 273a). During 1926 and 1927, the Dutch Phytopathological Service organised reports on weather and Potato Blight, the results of which confirmed van Everdingen's conclusions that it was possible to correlate outbreaks of this disease with certain weather conditions (273). As a result, the Royal Dutch Meteorological Institute at Te Bilt is carrying out observations and issuing warnings whenever conditions are such as to justify the expectation of an impending outbreak of Blight. Although Miss Löhnis (144) collected considerable data on the subject she did not succeed in establishing the existence of sufficient correlation to warrant the attempt to forecast epidemics. Van Everdingen (273), however, selected four conditions as enabling the onset of Potato Blight to be foretold:—(1) a night temperature below the dew point for four hours at least; (2) a temperature not falling below 10° C.; (3) a mean cloudiness on the following day of not less than 0·8; and (4) rainfall during the following twenty-four hours of at least 0·1 mm. These are the data upon which the Dutch forecasts of outbreaks of Potato Blight are at present based.

When " combined weather " effects on diseases are studied, it is seen that, however well each of the separate factorial relations is understood, the combined result is not known. Usually the only conclusions that can be arrived at are confined to statements such as that a disease is favoured by one of four possibilities :—hot and wet, hot and dry, cold and wet, and cold and dry. These also register variations from mean local weather, and, naturally, all the means will be different. Subjective human error is too strong to permit of success along such lines. Tehon (257) was the first to apply more scientific methods of correlating disease with phenology, and employed charts termed " hythergraphs." These are charts in which meteorological factors are measured in combination. Thus, the vertical scale represents temperatures and the horizontal scale rainfall. Tehon used Martin's data concerning Potato Blight, and, in replotting the combinations of temperature and rainfall, obtained a series of points which, when joined, formed curves that were circular, ovoid or elliptical, the curves being called " isopracts." In this way areas of various sizes were obtained which represented severe, mild, and no attacks of Potato Blight. By plotting temperature-rainfall data, and obtaining curves named " thermohyets," which represented the distribution-climate for certain diseases, he obtained areas outside of which the thermohyets did not correspond with the incidence of the diseases. Again, hythergraphs representing monthly or yearly disease-relations were obtained. An even more important feature was indicated by this method, namely, the relation of thermohyets to intensity of attack. Tehon plotted figures obtained over a series of years, each having a different mean index of Rust infection, along with the corresponding mean annual thermohyet. The points so plotted lay in two lines, called " trend lines." The points on each of these were plotted on the other by means of compasses, as well as on the line mid-way between and parallel to the trend lines ; and this line was called the line of true correlation. When the points corresponding to each index of infection were joined, curves were obtained which indicated the thermohyets of each index. In other words, by plotting a point in the graph indicating a forecasted thermohyetic, that point will lie between two fixed contour lines representing degrees of infection. Not only should it be possible by this method to forecast an epidemic outbreak but also the severity of infection. In order to do this, however, a standard must be fixed by which degrees of infection and of destructiveness can be measured. By the present method of personal estimation, scarcely any two observers would assign the same degree of infection for the same attacked plant.

Passing on to the problem of the provision of data, it must be evident that there is an enormous lack of detailed meteorological observations, possession of which would help to clear up many points. Up to the present the unit observation covers a large area, and consists, almost in every case, of temperature three times a

day and not at night (a very important time), rainfall, sunlight and humidity in the open air. Data which would be more useful are those concerning conditions existing in the crop, and only a few isolated workers have recorded such. Each factor in the crop will vary according to the type of crop plant. Roussakov (221) examined many of these points. He found that there were considerable differences between open-air temperatures and those of the air within the crop. The temperatures in the crop also varied according to the time of day or night, and the presence of clouds and rainfall. For example, the open air temperature in the daytime was lower than that in the midst of the crop by 1°–3° C., but was higher at 9 p.m. by 4°–6·5° C., while the two nearly coincided at 7 a.m. The highest temperature of all at 9 p.m. was at the surface level of bare land, and the lowest temperature at the same time was at a height of 90 cm. in the crop. The humidity varied greatly also, this being influenced by winds and by clouds. In a dry summer, the relative humidity was 85 per cent. near soil level, 72·5 per cent. at mid-crop height, and 67 per cent. at the top of the plants. In a wet summer, the relative humidity was more evenly distributed, that at the base of the crop being only 10 per cent. greater than that at the top. Since shading affects the temperature of the plants, as already explained in the section on light relations, and since humidity also does so, Roussakov's data relative to the penetration of sunlight into a crop are interesting. A crop of rye, with a fairly dense stand and from 150–160 cm. high allowed the following proportions of sunlight to penetrate :—

60–65 per cent.	sunlight	penetrated	down to	80–90 cm.	from soil level.
18–20 per cent.	,,	,,	25–30 cm.	,,	,,
10 per cent.	,,	,,	10–17 cm.	,,	,,
5 per cent.	,,	,,	5 cm.	,,	,,

Again, the details of distribution of spores by wind are imperfectly known. Little is known of the relative effects of the upper and lower air strata on spore viability, or concerning the possible length of suspension of spores in the air. For a few types of spores only has any relation of density to rate of fall been established in connection with the rate of deposit in winds of varying velocity.

Conclusion.

There are many questions that the plant pathologist might be expected to answer, and the first is whether he is sure that certain groups of meteorological factors do lead to epidemic outbreaks of a disease or group of diseases.

In view of what has been said above, there can be no doubt but that meteorological factors do determine to a great extent outbreaks and epidemics of most plant diseases.

The group of factors primarily concerned consists in most cases of temperature, moisture (and humidity), light and wind, the combination varying according to the disease.

A second question is whether there are certain very specific meteorological factors upon which a particular disease (or group of diseases) appears to depend. This can also be answered with certainty. Controlled research in the laboratory has demonstrated that each disease has a very definite range within each of the meteorological factors. In nature, however, the greater and more irregular variability of these factors makes correlation in the field very difficult. Further work and far more data are required before the ranges that prevail in the field can be estimated.

Following this, he may be asked, thirdly, to indicate with one particular disease, or with a few, what the exact factors and their duration are, and what particular coincidence of these factors is necessary for the occurrence of an epidemic.

Fortunately, it is possible to give a definite example. The Potato Blight, caused by *Phytophthora infestans*, depends upon a set of conditions which are very specific. These have already been laid down by van Everdingen, and are the result of much research and of years of work. They have been mentioned previously, but may be repeated here. For the outbreak of this disease there are necessary :—(1) a night temperature, of four hours' duration at least, below dew point ; (2) a temperature of not less than 10° C ; (3) a mean cloudiness on the following day not falling below 0·8 ; and (4) rainfall of at least 0·1 mm. during the following twenty-four hours.

Fourthly, the plant pathologist may be asked what are the data that are needed to determine accurately the phenology of plant diseases and what are the methods suggested for obtaining them ?

For each important crop plant during the whole period of its growth and maturation the following meteorological data are required :—

(1) Air temperatures : (*a*) above the crop ; (*b*) at the level of the top of the crop ; (*c*) at mid-crop height ; (*d*) at the base of the plants, and (*e*) in the soil. The temperatures should be recorded every two or three hours during the whole twenty-four hour period, or better still by a continuous method.

(2) The moisture content of the land : (*a*) bare, near the crop, and (*b*) under the crop ; the usual precipitation records, measured twice daily and nightly.

(3) The relative humidity of the air : (*a*) above the crop ; (*b*) at the level of the top of the crop ; (*c*) at each quarter of its height within the crop, and (*d*) at the base of the crop. That just over bare land is also required. The records should be taken every three hours, day and night, or preferably continuously.

(4) Cloud records and sunlight intensity ; also relative penetrations of sunlight, clear and shaded, into the crop plants, for each degree of density and height of the plants in the crop.

(5) The relative penetration of precipitation into a crop, at each degree of density, and the length of time moisture remains on the foliage.

(6) The relative amounts of dew deposition in crops, at different heights in the crop, and for each state of temperature, moisture, and humidity as well as of crop density.

(7) The relative penetration of wind of varying degrees of force into the crop, and its relation to crop humidity, temperature, and spore dispersal.

(8) The humidity and temperature of the higher air strata (100–15,000 ft.).

(9) More information relative to air currents and spore dispersal.

The methods to be employed for securing the data required cannot be left in better hands than those of the meteorologist himself. What is essential is a system of recording these data for each important crop plant in as many districts, climates and countries as possible. The British Empire offers plenty of scope as far as differences of climate are concerned.

If such a vast and varied array of meteorological data becomes available, the question will arise as to whose province it will be to correlate them with plant disease phenomena. If such correlation is to be done at all it is clear that the plant pathologist will have to stir himself and work out standardised methods by means of which " degrees of disease," or " epidemic intensity " can be measured with accuracy, and without any disturbing factor due to the subjectivity of the recorder. These standardised methods will perhaps differ for the diseases of different crops, and to devise them will be no easy task ; nor will their application in practice be possible except by those possessing almost an infinity of patience and perseverance. Limits of available space preclude the discussion of this matter here, but it may be said that in connection with the breeding of resistant varieties, particularly in the United States of America, some progress has already been made in formulating standards by means of which degrees of Rust attack on certain cereals can be recorded, so that accurate comparisons can be made.

Having secured meteorological data and those of disease intensity, the problem of correlation will become acute. Will the meteorologist or the plant pathologist or either of them be competent to carry out such correlation ? Or, will the task require a specialist " superman " in the form of a statistician ? The answer to such questions may perhaps be deferred for the present, but it may be pointed out that Tehon has already shown that the problem is one involving

deep analytical and higher mathematical treatment; and the humble present-day plant pathologist may well feel that such a task would be well beyond his powers. What searchings of heart, if any, the meteorologist might have in regard to the task it is not for a plant pathologist like the present writer to enquire.

The present paper has been an attempt to show that a relationship exists between plant pathology and meteorology, and to indicate some ways in which the study of that relationship might with profit be intensified. The theme has been based on, and illustrated exclusively by, existing plant pathological literature, but it is felt that in meteorological literature there may exist papers that would be of interest to plant pathologists in trying to solve their problems. If so, plant pathologists would be under a debt of gratitude to any meteorologist who would be good enough to bring such work to their notice.

The writer wishes to record his sincere thanks to both Dr. Butler and Dr. Pethybridge for their kind help and criticism, and to the former also for placing the use of the library of the Imperial Bureau of Mycology at his disposal.

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